

THREE NEW IDIOCERINE LEAFHOPPERS (HOMOPTERA: CICADELLIDAE) FROM GUYANA WITH NOTES ON ANT-MUTUALISM AND SUBSOCIALITY

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Abstract.—The species *Rotundicerus minutus* Dietrich, **NEW SPECIES**, *Rotundicerus rubripictus* Dietrich, **NEW SPECIES**, and *Chiasmodolon bhagwandum* Dietrich, **NEW GENUS** and **SPECIES**, all from Guyana, are described and illustrated. *Rotundicerus minutus* exhibits egg-guarding behavior and is tended by ants. Three other Guyanese idiocerines, *Chunroides knighti* Maldonado-Capriles, *Hyalocerus* sp., and *Luteobalmus* sp., are also ant-attended, the first occurring in shelters constructed by the ants. The relationships among active, sessile, ant-mutualistic, and subsocial behaviors are discussed with reference to the evolution of the Cicadelloidea and Membracoidea.

Key Words: Ant-leafhopper mutualism, egg-guarding, subsocial behavior, Idiocerinae, Membracoidea, Formicidae

While studying ant-mutualistic and subsocial (*sensu* Wilson 1971) treehoppers (Membracoidea) in the Republic of Guyana, we observed four species of idiocerine leafhoppers in similar situations exhibiting these same behaviors.

Ant-mutualism occurs in several groups of auchenorrhynchous Homoptera, including Fulgoroidea—families Tettigometridae (Lesne 1905), Issidae (Delpino 1875), Delphacidae (Krishna Ayyar 1935; *Peregrinus maidis* Ashmead (as *Pundaluoya simplicia*), and Cixiidae (Myers 1929; *Anemosyne cubana* Stål)—and Cercopidae (Mann 1915), in which the homopterans occur in the nests of the ants. The only known occurrence of ant-fulgoroid mutualism outside the ants' nest is an observation (Dietrich, unpublished) of *Picumna* sp. issids being tended

by formicine ants on the twigs of two unidentified hosts in southern Mexico. Similarly, in some Membracoidea and Cicadelloidea (*sensu* Evans 1947, 1948), ants collect honeydew from the homopterans on the leaves and stems of their host plant. Ant-attendance is common in the Membracoidea and this group is unusual in having numerous subsocial species—i.e. females guard their eggs (Haviland 1925, Hinton 1977, Brown 1976, Bristow 1983, McEvoy 1979, Wood 1984, S.H.M. and C.H.D., unpublished observations).

Reports of ant-leafhopper mutualism are rare in the literature, and egg-guarding behavior has apparently never been documented among the Cicadelloidea. Bergevin (1910) reported ant-attendance of nymphs and adults of the macropsine *Hephathus nanus* (Herrich-Schaffer) in North Africa. Shortly thereafter, Lamborn (1914) gave a detailed account of ant-mutualism for the West African agalline *Nehela ornata* Dis-

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tant including a description of ant-constructed shelters containing the leafhoppers. Other reports of ant-leafhopper mutualism involve several species of the macropsine genus *Macropsis* (Viraktamath 1980), the ledrine *Petaloccephala nigrilinea* Walker (Chatterjee 1934), the iassine *Hishimonus viraktamathi* Knight (Knight 1973), all from India, and members of the Australian cicadelloid family Eurymelidae (Evans 1931). Previous documentation of ant-leafhopper mutualism in the New World is apparently limited to the observations by Beamer and Michener (1950) and Lavigne (1966) of ants tending *Hecalus* (as *Parabolocratus*) spp. (Hecalinae) in Kansas and by Wheeler (1921) of ants tending "jassids" in Guyana (then British Guiana).

We observed four species of idiocerine leafhoppers being tended by ants, at least two of which were apparently also subsocial. One of these was identified as *Chunroides knighti* Maldonado-Capriles. A second species could not be identified based on existing keys and descriptions (see Maldonado-Capriles 1984 for review) and is here described as new and placed in the previously monotypic genus *Rotundicerus* Maldonado-Capriles. The other two ant-attended species, *Hyalocerus* sp. and *Luteobalmus* sp., are also apparently undescribed, but were represented only by females and are not described here.

Two additional idiocerine species were collected at blacklights in Guyana. Both of these also proved to be new, one representing a new genus, and are described below.

Acronyms for collections in which the specimens used in this study are deposited are as follows: NCSU (Insect Collection, North Carolina State University, Raleigh); SHMC (Stuart H. McKamey collection), USNM (United States National Museum of Natural History). In quotations of label data, a virgule (/) separates lines on a label and a semicolon separates information on different labels. Morphological terminology fol-

lows that of Maldonado-Capriles (1977a, b, 1984).

***Rotundicerus minutus* Dietrich,**

NEW SPECIES

(Figs. 1–9, 29)

Diagnosis.—This species is much smaller than *Rotundicerus luteus* Maldonado-Capriles and also differs in having characteristic white marks on the forewing membrane, a relatively short ovipositor, and distinctive male genitalia.

Description (males and females).—*Color:* Dull yellow with anterior half of scutellum, thoracic venter, and, in some specimens, femora and ventral part of face dark brown; forewing membrane yellow-hyaline, usually with white marks in inner anteapical cell, along claval suture, and at claval apex, veins and membrane variably infused with dark brown. *Head* (Figs. 1, 2): Face strongly and evenly convex, clypellus constricted medially, approximately $1.33\times$ longer than its apical width, apex slightly narrower than base; lateral margins of genae weakly angulate just ventrad of eyes; upper frontal sutures extending to point directly ventrad of mesal ocellar margins; distance between ocelli about $1.33\times$ distance from ocellus to eye; vertex, in dorsal view, about $3.33\times$ wider than long. *Thorax* (Figs. 2, 3): Visible part of pronotum about $3.4\times$ wider than long in dorsal view; scutellum approximately $1.4\times$ wider than long, in lateral view strongly convex anteriorly; forewing (Fig. 3) with 2 costal, 4 apical, 2 anteapical, and 2 discal cells; inner apical and outer anteapical cells not meeting, separated by a short crossvein; metathoracic femur with small conical projection on upper adlateral surface of base; metathoracic tibial rows I–III with 7–8, 4, and 4–5 stout spines, respectively, row IV with 20+ pale oblanccolate setae; metathoracic tarsomeres I and II with 4–5 and 3–4 cucullate setae, respectively, at apices of plantar surfaces. *Male genitalia* (Figs. 4–9): Pygofer (Fig. 4) with anterior apodemes absent; tergum X with ventral

appendices straight, not L-shaped; subgenital plate (Figs. 4, 5) with apical half, in lateral view, strongly arcuate, dorsal margin with numerous long, fine setae; aedeagus (Figs. 7, 8), in lateral view, with shaft evenly curved anterodorsally, anterior face crenate, in posterior view with shaft widened medially and tapering towards apex; connective (Fig. 6) triangular, lateral ridges forming V-shape and with conical anterodorsal projection; style (Figs. 6, 8, 9) with dorsal setiferous hump, preapical process bulbous and setiferous, apical process acute, arched posteroventrally, in posterior view projecting dorsolaterally. *Female genitalia*: Ovipositor only slightly surpassing apex of pygofer. *Measurements* (mm): body length (to apex of forewing) 2.8–3.1; face length 0.9–1.0, width 1.0–1.1; pronotum width 1.0–1.1; forewing length 2.2–2.4; prothoracic tibia length 0.5–0.6; metathoracic tibia length 1.0–1.1; male plate length 0.5; ovipositor length 1.0.

Material examined.—Holotype male labeled: "GUYANA: Demerara/Co., ca 5 km N of/Kairuni Creek./G'town-Linden: Hwy, ca km 71, 3/Aug 1987, ca 50 m/C. H. Dietrich; C. H. Dietrich/lot # 87-559; DIETRICH RES./16-88-348e ♂; HOLOTYPE/Rotundicerus/minutus/Dietrich (USNM, on indefinite loan from NCSU). Other material: 1 male and 6 female paratypes from same locality (NCSU); one additional male and female from Bartica, Mazaruni-Potaro, Guyana (SHMC).

Notes.—This species keys to *Rotundicerus* in Maldonado-Capriles' (1984) key to Neotropical genera. The feature, "ocelli set apart at 2× the distance from ocellus to eye," attributed to this genus therein, is contradicted by Maldonado-Capriles' (1977a) original description and figure of the genus, as well as the condition in *R. minutus*. The semicircular subgenital plate of *R. minutus* resembles that of *Parachunroides* Maldonado-Capriles, but the form of the male genitalia indicates that the new species is more closely related to *R. luteus* Maldonado-Ca-

priles. The trivial name refers to the small size of *R. minutus* relative to its congeners.

Biology.—Based on several sets of observations of ants, reared mymarids, parental females, egg masses, and aggregations of nymphs and adults, we infer the following developmental sequence for *R. minutus*: eggs are inserted almost completely into the stem of woody hosts. The egg mass consists of several close, mostly longitudinal incisions. In some cases, many females oviposit very near each other. The parental female remains atop the egg mass (Fig. 29), unyielding to disturbances. Mymarid parasitoids nonetheless are able to attack some of the eggs. After eclosion, the non-jumping nymphs remain loosely aggregated in the vicinity of the parent. This species was observed on two plant species, being tended by workers of the ant species *Camponotus femoratus* (Fabricius) and *Crematogaster* sp. In one instance, these leafhoppers were associated with a large aggregation of *Tropidaspis* sp. (Membracoidea: Biturritiidae (= Lampropteridae *sensu* Evans 1948)).

***Rotundicerus rubripictus* Dietrich,
NEW SPECIES
(Figs. 10–19)**

Diagnosis.—This species differs from its congeners in the presence of distinct green and red markings on the head and thorax and the distinctive form of the male genitalia.

Description (males and females).—*Color*: Dorsal part of face, vertex and pronotum green with 2 prominent red longitudinal stripes, pronotum with second pair of sub-lateral red patches; scutellum cream colored, infused with green and with yellowish medial patch and yellowish triangular mark at each anterior corner; forewing smoky hyaline, variably infused with white, veins and membrane marked with dark brown (Fig. 12), clavus with red basal stripe flanked by green stripe that extends to suture, area between claval suture and vein Cu red ba-

sally; remainder of body yellow to light brown. *Head* (Figs. 10, 11): Face strongly convex, about $1.2\times$ wider than long; clypellus inflexed medially, apex slightly produced; genae with lateral margins slightly inflexed, with short, stout, pale seta ventrad of each eye; antennal flagellum with 2 long subbasal trichoid sensilla; distance between ocelli about $2\times$ distance from ocellus to eye; vertex about $2.25\times$ wider than medial length. *Thorax* (Figs. 11, 12): Pronotum about $2.4\times$ wider than medial length; scutellum about $1.4\times$ wider than long, in lateral view appearing more or less flat; forewing (Fig. 12) with apical cell III lacking basal crossvein; metathoracic tibia setal rows I–III with 12–14, 6, and 5–6 spurs, respectively, row IV with numerous pale oblan-ceolate setae each paired with a short seta $0.25\text{--}0.33\times$ as long; metathoracic tarsomeres I and II with 5 and 4 apical cucullate setae, respectively, on plantar surfaces, tarsomere I with dorsoapical pair of setae. *Male genitalia* (Figs. 13–19): Pygofer (Fig. 13) with pair of broad dorsal anterior apodemes, posterior membranous area bounded ventrolaterally by sclerotized ridge with short dorsoapical projection and small oval sclerotized apical plate (Fig. 15), membranous area with numerous short darkly pigmented setae; tergum X (Fig. 13) with distinct ventrolateral emargination and hooked basolateral appendix; plate (Fig. 14) with apex slightly compressed and bearing a few stout setae; aedeagus (Figs. 17, 18) short with apex acute and curved anterodorsally, apical third crenate posteriorly, ventral process in posterior view ovoid; style (Figs. 16, 18, 19) with dorsal setiferous hump, preapical process bearing a few stout setae, apex directed dorsolaterally; connective (Fig. 16) somewhat flattened, with small, acute postero-dorsal knob. *Female genitalia*: Ovipositor exceeding apex of pygofer by about $2\times$ ovipositor width. *Measurements* (mm): Body length 3.9–4.1; face length 1.4, width 1.6; pronotum width 1.4–1.5; forewing length 3.3–3.4; prothoracic tibia length 0.8; meta-

thoracic tibia length 1.5, male plate length 0.5; ovipositor length 1.4.

Material examined.—Holotype male labeled: "GUYANA: Mazaruni/Potaro, Isl. ca 35/air km SW Bartica; ca 95 m, 17–18 July/1987, C. H. Dietrich; DIETRICH RES./14-89-15i ♂; HOLOTYPE/Rotundicerus/ rubripictus/ Dietrich" (USNM, on indefinite loan from NCSU). Other material: 3 female paratypes, same data (all NCSU).

Notes.—The presence of a stout seta below the eye of *Rotundicerus rubripictus* suggests that the species might be placed in *Optocerus* Freytag. Nevertheless, the structure of the male genitalia and wing venation, which differ drastically from the type of *Optocerus*, are so similar to those of *R. luteus* Maldonado-Capriles, that the new species' more appropriate placement appears to be in *Rotundicerus*.

The type-series was collected at a black-light on a forested island in the Mazaruni River near Bartica, Guyana. The trivial name refers to the red patches on the head and thorax.

Chiasmodolon Dietrich, NEW GENUS

Type species: *Chiasmodolon bhagwandomorum* Dietrich.

Diagnosis.—These leafhoppers would key out to *Chileanoscopus* Freytag in Maldonado-Capriles' (1984) key to Neotropical genera. However, they lack subapical setae on the hind femora and differ sufficiently in other respects from *Chileanoscopus* and other described Neotropical genera to warrant their placement in a new genus. The following combination of diagnostic characters should distinguish *Chiasmodolon* from other Idiocerinae: coloration not mottled, face flattened and as wide as long, forewings hyaline with veins dark and with 2 anteapical cells, the outer cell not widened apically, male pygofer with pair of mesally directed blade-like projections, aedeagus without crenulations or lateral processes.

Description (males and females).—*Color*: Yellowish, with sparse obscure brown markings; forewings smoky hyaline, veins dark. *Head* (Figs. 20, 21): Face about as wide as long, flattened medially, with 1 or 2 small setae on genal margins just ventrad of each eye; lorae extending to ventral margins of genae; clypellus with margins subparallel, slightly inflexed; antennal flagellum with 2 long subbasal trichoid sensilla. *Thorax* (Figs. 21, 22): Scutellum only slightly convex; forewing with 2 anteapical and 4 apical cells, outer anteapical cell not widened towards apex, outer apical cell with base acute, apical cell II parallel-sided; metathoracic femur without subapical seta; metathoracic tibial row IV with numerous long, pale ob lanceolate setae, each paired with a short seta about half as long. *Male genitalia* (Figs. 23–28): Pygofer with pair of acute, mesally projecting crossed processes on dorsum just posterad of base of tergum X, each lateroapical margin produced into an auriculate process; subgenital plate somewhat compressed apically, apex bearing stout setae; aedeagus smooth and narrow, without crenulations or lateral processes, base of shaft with dorsal and ventral processes, apex acuminate; style with prominent preapical process bearing stout setae and a dorsal setiferous hump; connective with dorsal anteriorly acuminate keel. *Female genitalia*: Ovipositor exceeding pygofer by about $2\times$ ventral width of ovipositor.

Chiasmodolon bhagwandum Dietrich,

NEW SPECIES

(Figs. 20–28)

Description (males and females).—*Color*: As described for genus; clypeus with 7 sub-lateral brown dashes, brown dash below each ocellus at apex of upper frontal suture, brown spot laterad of each ocellus and a brown patch between ocelli; ocelli bordered with brown; narrow brown medial stripe extending from face between ocelli over vertex to posterior margin of pronotum, pair of wider

diagonal stripes extending from just dorsad of ocellus dorsolaterally to posterior margin of vertex; scutellum with 2 anterolateral brown triangles and distinct black mark near midpoint of lateral margin; forewing with distinct black mark near base of corium; first abdominal sternum yellow, remainder brown. *Head* (Figs. 20, 21): Face as wide as long, genae nearly straight, with slight notch just ventrad of mesal margin of eye; vertex about $6\times$ wider than median length. *Thorax*: Pronotum about $2.6\times$ wider than long, scutellum slightly shorter than wide; forewing as described for genus, costal margin infused with yellow-green opaque sclerotization; metathoracic tibia with rows I–III with 22–23, 7–8, and 8–9 stout spurs, respectively, row IV as described for genus, with 3–5 relatively stout subapical setae; metathoracic tarsomeres I and II with 5 and 4 apical cucullate setae, respectively, on plantar surfaces, tarsomere I with a dorsoapical pair of setae. *Male genitalia* (Figs. 23–28): Pygofer (Fig. 23) as described for genus, anterior apodemes broad; tergum X not modified; plate (Fig. 24) with 2 or 3 stout apical setae in addition to numerous fine setae on dorsal margin; aedeagus (Figs. 26, 27) in lateral view sinuate, anterior process in posterior view parallel-sided; style (Figs. 25, 27, 28) with preapical process bearing 2 relatively stout setae. *Female genitalia*: As described for genus. *Measurements* (mm): Body length 6.2–6.5; face length 2.3–2.4, width 2.3–2.4; pronotum width 1.9–2.1; forewing length 5.4–5.5; prothoracic tibia length 1.4; metathoracic tibia length 2.4–2.7; male plate length 0.8; ovipositor length 1.3.

Material examined.—Holotype male labeled: "GUYANA: Mazaruni/Potaro, Isl. ca 35/air km SW Bartica: 95 m, 17–18 July/1987, C. H. Dietrich; Dietrich Res./14-89-15f ♂; HOLOTYPE/*Chiasmodolon/bhagwandum*/Dietrich" (USNM, on indefinite loan from NCSU). Other material: 1 male and 1 female paratype, same data (both NCSU).

Notes.—*C. bhagwandorum* was collected at a blacklight on a forested island in the Mazaruni River, Guyana. The genus name was formed by combining the Greek adjective, *chiasmōs*, meaning crosswise, with the masculine noun, *dolon*, meaning dagger, and refers to the crossed knife-like structures on the dorsum of the male pygofer. The species is named in honor of the Bhagwandas family of Bartica, Guyana, whose generous assistance made possible the collection of the type-series.

BEHAVIORAL OBSERVATIONS ON OTHER NEOTROPICAL IDOCERINAE

We observed ant-attendance in four species of idiocerine leafhoppers, at least two of which are also apparently subsocial. In addition to *Rotundicerus minutus* (discussed above), we observed a female of *Hyalocerus* sp. (S.H.M. lot# 87-133a) with a large aggregation of nymphs being tended by *Crematogaster* sp. ants. Apparently, this leafhopper exhibits subsocial behavior similar to that described for *R. minutus*. Two adult males and several nymphs of a third idiocerine, *Chunroides knighti*, were found in a shelter constructed of decayed plant material by the tending *Azteca* sp. ants on the stem of a small woody shrub with large, ovoid leaves and latex sap. Finally, a female of *Luteobalmus* sp. was observed being tended by ants of the genus *Ectatomma*.

DISCUSSION

While ant-mutualistic and sessile (non-jumping) behavior both appear to correspond with subsociality in the Membracoidea (Membracidae, Aetalionidae, Biturittiidae, and Nicomiidae) and Cicadelloidea (Cicadellidae and Eurymelidae), the pattern of this correspondence differs between the two superfamilies.

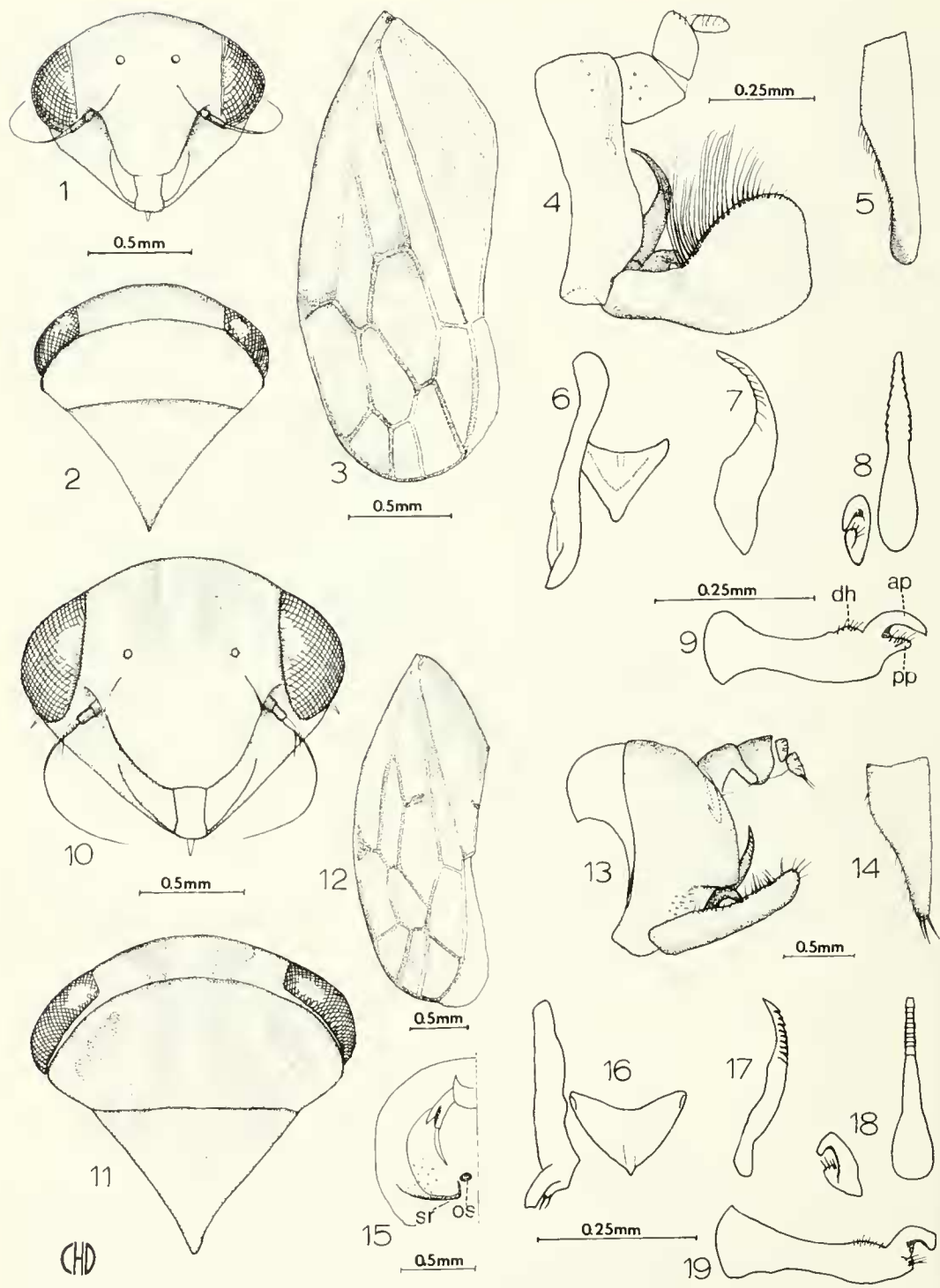
As far as is known, all membracoids have sessile nymphs. Sessile behavior assures a relatively stable source of "honey-dew," and thus may have arisen in Membracoidea as

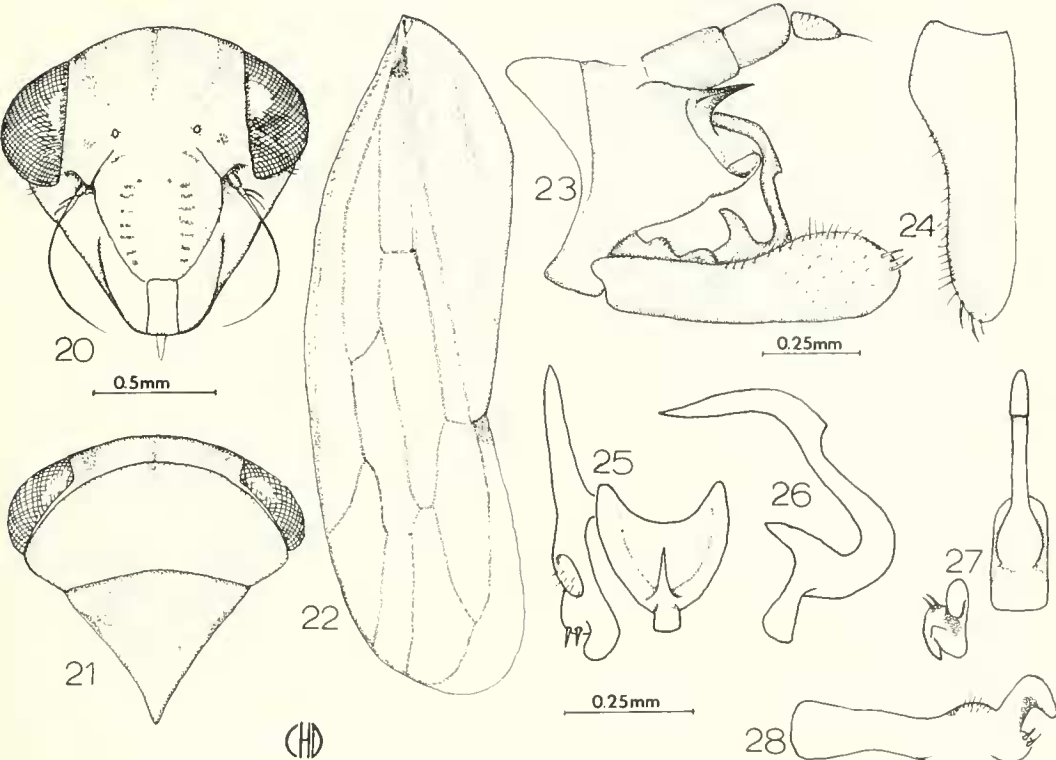
a coevolutionary response to the opportunistic ants abundant in lowland, wet tropical forests (Wood 1982, 1984). In some situations, subsociality would subsequently be favored due, as Wood (1984) suggested, to selection for gregarious behavior, because aggregations would provide a more attractive and stable resource for ants. Evidently, ant-attendance was lost in some membracoid groups while their sessile behavior persisted, perhaps facilitated by the evolution of such alternative predator-avoidance strategies as crypsis or aposematic coloration.

In contrast, as far as is known (Beamer and Michener 1950, Evans 1988), most Cicadelloidea have nymphs capable of jumping when disturbed and are neither ant-attended nor subsocial. Thus, while the Eurymelidae and Ulopinae, generally considered to be among the more primitive cicadelloids (Evans 1947, Nielson 1985—see Hamilton 1983 for an alternative classification), have sessile nymphs, suggesting that the ancestral cicadelloid was sessile, this habit was apparently lost early in the evolution of the superfamily. Although most of the cicadellid species in which ant-mutualistic and subsocial behaviors are found belong to subfamilies generally thought to be primitive to moderately primitive (Nielson 1985), their apparent taxonomically disjunct incidence among the Cicadellidae suggests multiple derivations of these behaviors. Further studies of the life-histories of Cicadelloidea, especially of the plesiomorphic groups, are needed to elucidate the relationships among solitary, sessile, gregarious, ant-mutualistic, and subsocial behaviors and their role in the evolution of this group.

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Figs. 20–28. *Chiasmodolon bhagwandorum* Dietrich, new species. 20, Head, anterior view; 21, head, pronotum, and scutellum, dorsal view; 22, left forewing. 23–28 Male genitalia. 23, Genital capsule, lateral view; 24, plate, ventral view; 25, left style and connective, dorsal view; 26, aedeagus, lateral view; 27, aedeagus and left style, posterior view; 28, style, lateral view.

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Figs. 1–19. 1–9, *Rotundicerus minutus* Dietrich, new species. 1, Head, anterior view; 2, head, pronotum, and scutellum, dorsal view; 3, left forewing. 4–9, Male genitalia. 4, Genital capsule, lateral view; 5, subgenital plate, ventral view; 6, left style and connective, dorsal view; 7, aedeagus, lateral view; 8, aedeagus and left style, posterior view; 9, style, lateral view. ap, apical process; dh, dorsal hump; pp, preapical process. Figs. 10–19, *Rotundicerus rubripictus* Dietrich, new species. 10, Head, anterior view; 11, head, pronotum, and scutellum, dorsal view; 12, left forewing. 13–19, Male genitalia. 13, Genital capsule, lateral view; 14, subgenital plate, ventral view; 15, genital capsule (in part), posterior view; 16, left style and connective, dorsal view; 17, aedeagus, lateral view; 18, aedeagus and left style, posterior view; 19, style, lateral view. ha, hooked appendix; os, oval sclerite; sr, sclerotized ridge.

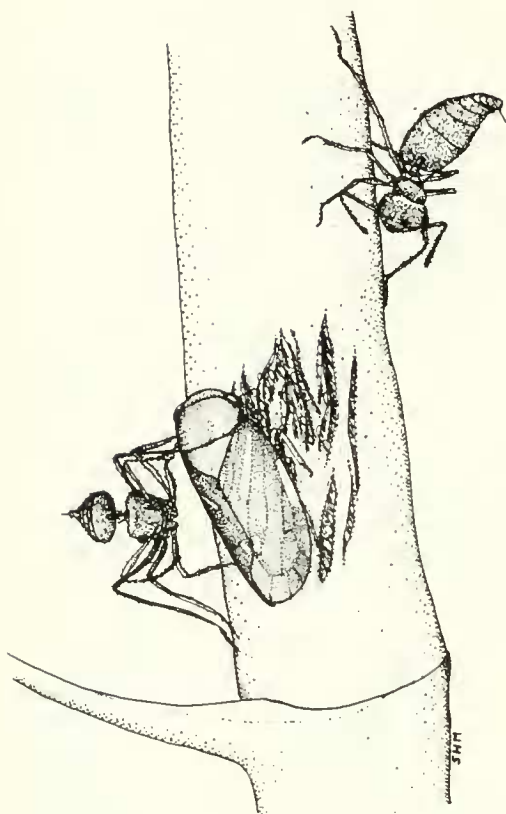


Fig. 29. *Rotundicerus minutus* female, guarding egg mass while tended by *Crematogaster* ants. (Drawn from photograph.)

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